

RECENT ADVANCES IN FISH GEOGRAPHY OF INDIA¹

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(With sixteen figures)

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INTRODUCTION

I greatly appreciate the honour, which the Council of the Bombay Natural History Society has done me in inviting me to deliver an address on the occasion of the Annual General Meeting. I am very thankful to them for the invitation. The choice of the subject has been influenced by two main considerations. Firstly, at the Annual General Meeting of the Society in 1948, I gave to the members an idea of the Satpura Hypothesis concerning the distribution of the so-called Malayan plants and animals to Peninsular India. Secondly, in view of repeated references to this Hypothesis in the *Journal*, your energetic editor, Mr. Sálím Ali, has been requesting me to sum up in a popular form, for the benefit of Indian naturalists, the main findings of the Satpura Hypothesis. As great advances have been made since 1948 in our conception of the Hypothesis, I have thought it worth while to place before you some aspects of biogeography, mainly based on the distribution of fishes, which have shed a great deal of light on the palaeogeography and palaeoclimates of India. Though some of our findings will also be applicable to terrestrial plants and animals, it must be clearly understood that the Satpura Hypothesis was proposed and has since been intensely investigated only with regard to the fishes of the torrential streams, which, on account of specialized ecological features of their habitats, have restricted means of dispersal (Hora, 1947).

¹ Text of the lecture delivered at the Annual General Meeting of the Bombay Natural History Society on 29th July, 1952, at 6 p.m.

HISTORY OF INDIAN FRESHWATER FISH FAUNA

The first record of an Indian freshwater fish is found in the Maleri beds of the Godavari Valley. These beds are of the Upper Triassic age and are thus as old as 170 million years. The Dipnoan or Lung-Fishes of the extinct genus *Ceratodus* were the only Indian fresh-



Fig. 1. The Dipnoan fish *Ceratodus* (*Neoceratodus forsteri* from Cambridge Natural History, 7, p. 509, 1904).

water fishes of that period. As the name implies, they are double breathers, i.e., capable of breathing with gills under water and of utilising atmospheric air for respiration through the air-bladder modified as lungs. They were thus marsh-loving fishes associated with large rivers which flooded extensive areas at times to produce marshy conditions. No Lung-fish is found in India today, though forms allied to *Ceratodus* are living in Queensland (Australia), South Africa and



Fig. 2. Present-day distribution of the Dipnoan fishes (from Cambridge Natural History, 7, p. 512, 1904).

South America. Such a discontinuous distribution of these fishes shows their great antiquity.

Where from did the Dipnoan fishes come to India and why did they die out here are the two obvious questions, which must be answered at this stage. During the Upper Triassic, there was a northern continent, the Angara (comprising part of Asia, Europe and North America), and a southern continent, the Gondwana (comprising Australia, southern Asia, Africa and South America). These two continents were separated by seas but had a land bridge, the 'Assam Link', between China and India. The Lung-fishes would appear to have evolved during the Middle Devonian period (325 million years) in North America and Europe and later migrated to the Gondwana continent over the 'Assam Link'. From India as centre, they got dispersed to Australia, Africa and South America. Upper Triassic was a period of great desiccation in India so the fishes

died out altogether, but they continued to live in suitable ecological pockets in other parts of the world. Those interested in more detailed

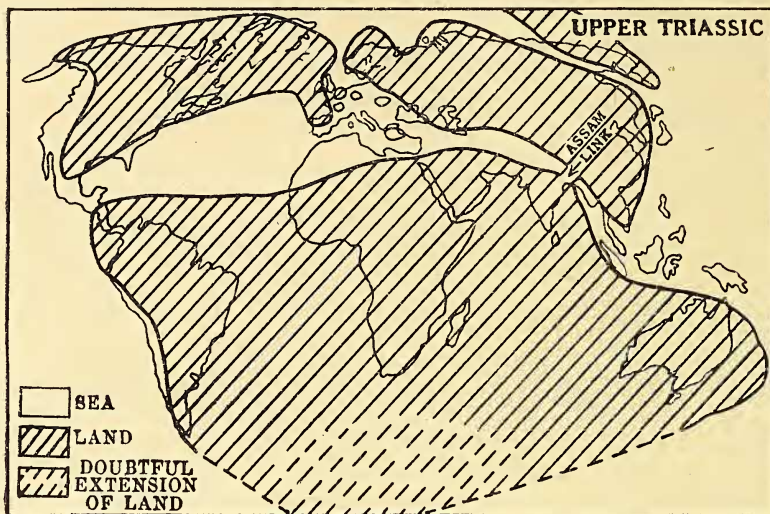


Fig. 3. The Continents of Angara and Gondwana during the Upper Trias. (Modified from Seward's map in *Plant Life through Ages*, 1931).

knowledge about the Indian Dipnoan fishes may see Hora and Menon, 1952.

On the return of moister conditions during the Jurassic period (145 million years), there was again an invasion of freshwater fishes

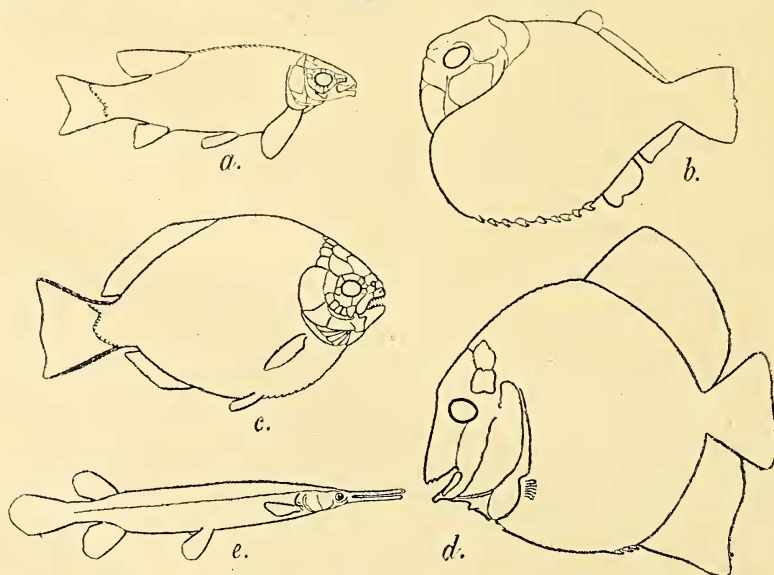


Fig. 4. The Ganoid fishes of India. (a) *Lepidodus*, (b) *Tetragonolepis*, (c) *Dapedius*, (d) A Pycnodont fish, (e) *Lepidosteus*.

from the Angara to the Gondwana over the 'Assam Link'. This time the Ganoids or Enamel-scaled fishes of the extinct genera *Lepidotus*, *Tetragonolepis* and *Dapedius* colonised Indian freshwaters and dispersed to Australia, Africa and South America in the same way as the Dipnoans did before them. Another period of desiccation completely wiped off this stock also, though their near relations are still living in other parts of the world. The fossil remains of the above genera are now known from the Kota beds in the Godavari Valley.

Wet conditions returned again during the Cretaceous period (120 million years) and the Ganoid fishes of the genera *Pycnodus* and *Lepidosteus* colonised the Indian freshwaters once again. They, however, became entombed in the extensive lava flows of the Upper Cretaceous. Their fossils are known from the Lameta beds at

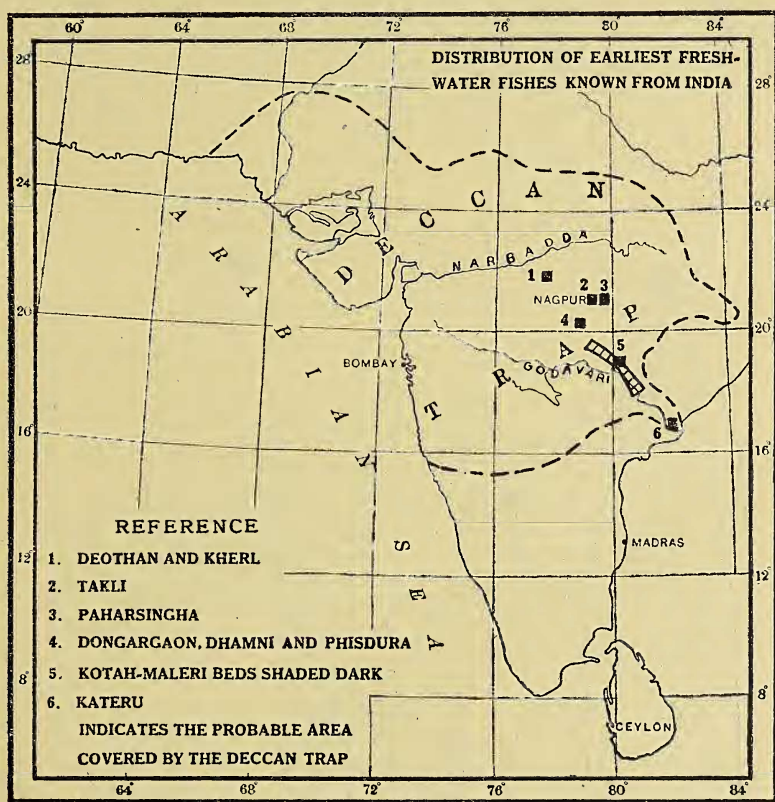


Fig. 5. Map of India showing the probable area of Deccan Trap and the distribution of freshwater fossil fish bearing beds of the Triassic, Jurassic, Cretaceous and the Eocene periods. After S. L. Hora (*Proc. Nat. Inst. Sci. India*, 4 (4), p. 398, 1938).

Dongargaon in Madhya Pradesh. These fishes also spread in the same way as those of the earlier two invasions.

When the volcanic activities had subsided and normal conditions had returned in the early Eocene (60 million years), the existence of

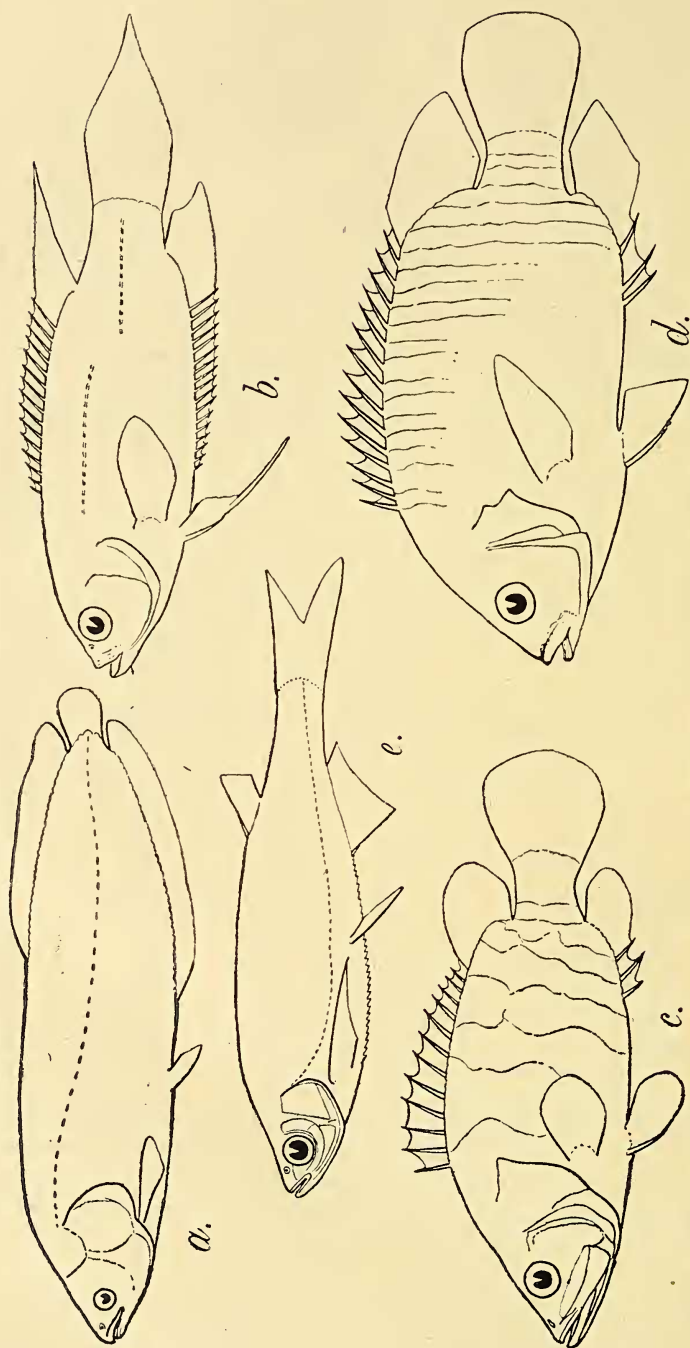


Fig. 6. The fossil Eocene fishes of India. (a) *Osteoglossid* fish, (b) *Polynacanthus*, (c) *Naudus*, (d) *Pristolepis*, (e) *Chela*.

the 'Assam Link' permitted another invasion of freshwater fishes from the mainland of Asia. The Ganoid fish *Lepidosteus* and certain

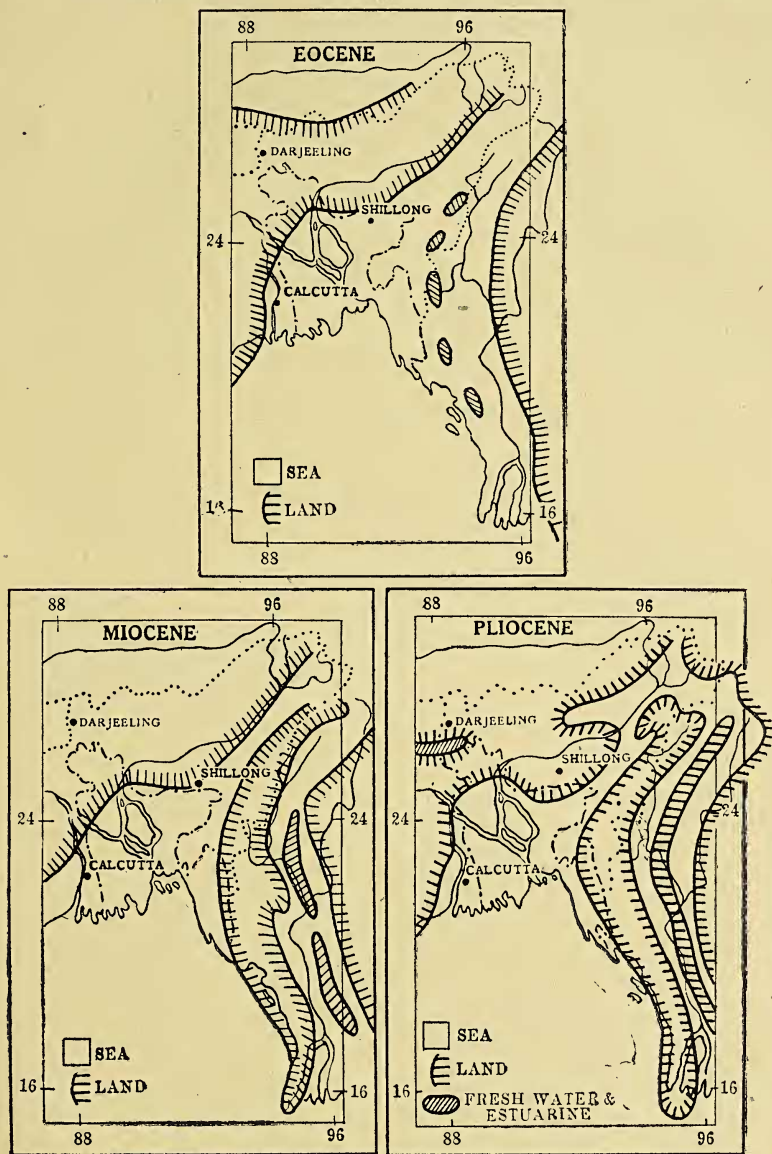


Fig. 7. Transgression of the Bay of Bengal during the Eocene, Miocene and Pliocene periods (Modified from Dr. M. S. Krishnan's maps).

Teleostean fishes of the families Osteoglossidae, Cyprinidae, Anabantidae and Nandidae colonised Indian waters but the Gondwana continent had become partly dismembered by then and there was no land connection between India and Australia, though land connections

between India and Africa and between Africa and South America are indicated by the distribution of fishes of that period. These earlier fishes are now represented by their fossil remains at Deothan, Kheri, Takli and Paharsingha in Madhya Pradesh. This fauna became entombed in the successive volcanic eruptions of the Eocene and it appears that during the Middle Eocene, the 'Assam Link' gave way due to the transgression of the Bay of Bengal northwards. The earlier fauna having been completely annihilated, the chances of further invasions also became nil owing to the extension of the sea. There are accordingly no fossil records of freshwater fishes for the whole of the Miocene period (25 million years). As a result of the Himalayan orogenic movements of the Pliocene (12 million years), a continuous arc of Himalayan-Alpine System seems to have been established for the spread of certain hill-stream fishes. Also Siwalik ecological conditions became established at the base of these hills and these facilitated the dispersal of marsh-loving Siluroid fishes of the genera *Chrysichthys*, *Mystus*, *Rita*, *Bagarius*, *Clarias*, *Heterobranchus*, etc.

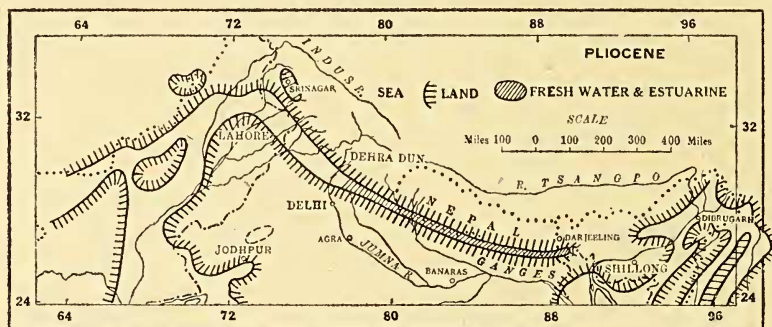


Fig. 8. The Siwalik gulf of the Pliocene (Modified from Dr. Krishnan's maps).

and of the Ophicephalid fishes. It would thus appear that the Carps, which form the most predominant group of the Indian freshwater fishes had not colonised Indian waters during the Pliocene, the reason being the brackish waters at the head of the receding Bay of Bengal of that period. Further orogenic movements during the Pleistocene, combined with successive waves of glaciation during the last million years facilitated movements of freshwater fishes from east to west but the later invasions did not extend beyond India to Africa. It will thus be seen that almost the entire freshwater fish-fauna of India consists of the Pleistocene migrants or of their modified descendants. The problems of fish geography, arising out of the present-day distribution of Indian fishes, are, therefore, of the Pleistocene period only and we shall now examine them one by one.

PROBLEMS OF FISH GEOGRAPHY OF INDIA

Taking into consideration the broader aspects of the distribution of the present-day freshwater fishes of India, one can enunciate the following problems that need elucidation:—

- i. Uniformity of the fish-fauna of the Indus and the Ganga river systems.

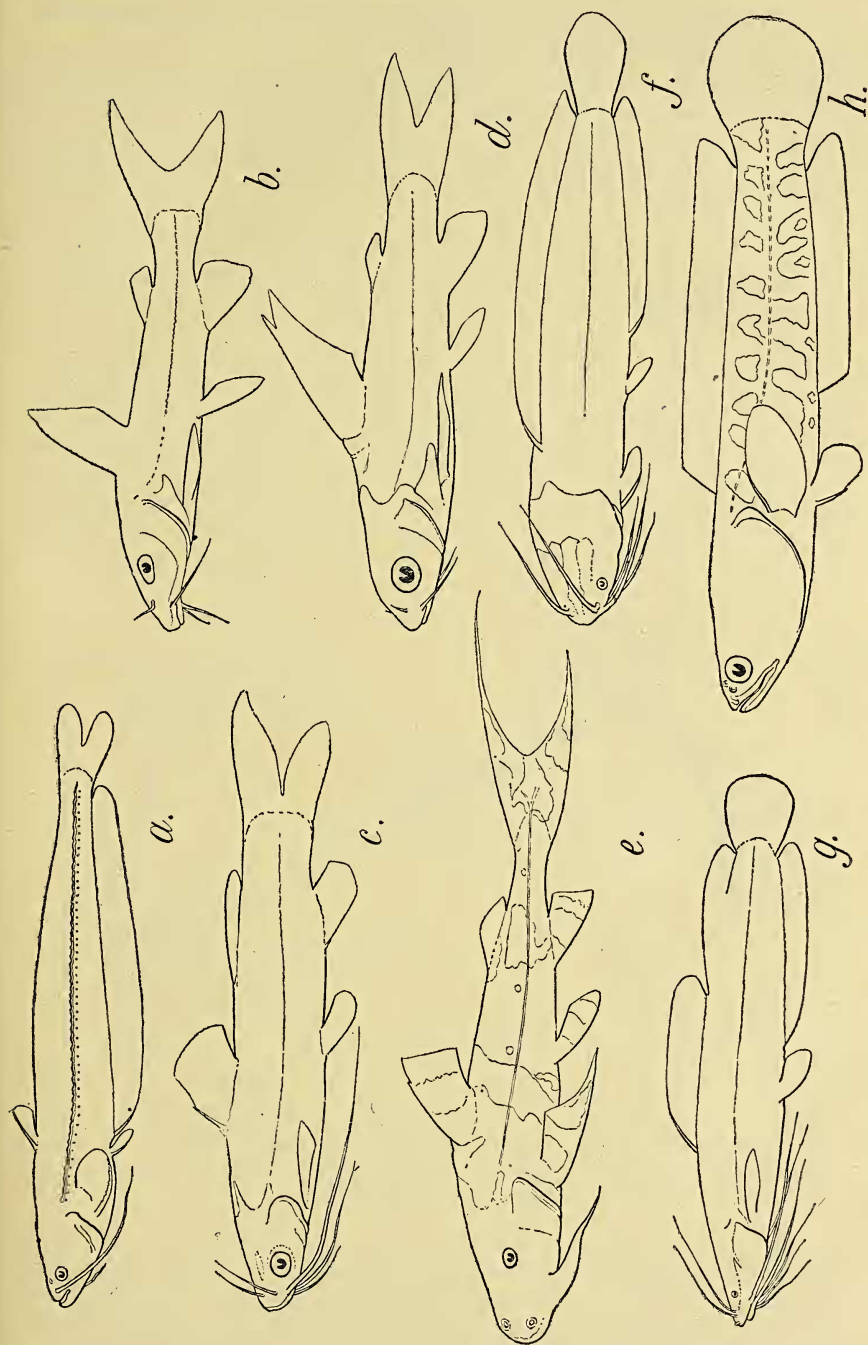


Fig. 9. The fossil Pliocene fishes of India. (a) *Silurus*, (b) *Chrysichthys*, (c) *Mystus*, (d) *Riba*, (e) *Bagarius*, (f) *Clarias*, (g) *Heterobranchius*, (h) *Ophicephalus*.

- ii. Extension of the Indo-Gangetic fish-fauna into the Mahanadi and Godavari river systems.
 - iii. Occurrence of the so-called Malayan forms in the Western Ghats and the Satpura trend of mountains.
 - iv. Dispersal of the fish-fauna of the Western Ghats to the Eastern Ghats, Orissa Hills, Aravalli Range, Satpura and Vindhya Ranges.
 - v. Occurrence of the Sind fish-fauna in the Aravalli Range.
 - vi. Absence of the so-called Malayan forms in the Western Himalayas.
- i. *Uniformity of the fish-fauna of the Indus and the Ganga river systems.*—I have referred above (p. 176, text fig. 8) to the Siwalik Gulf, which stretched as a narrow arm of the sea at the base of the young Himalayas during the Pliocene and received the drainage of the southern face of the Himalayas. As shown in the figure, a considerable part of it towards the east contained freshwater in which lived the Siluroid fishes of the Pliocene referred to above. The sediments deposited at the bottom of this gulf ultimately formed the

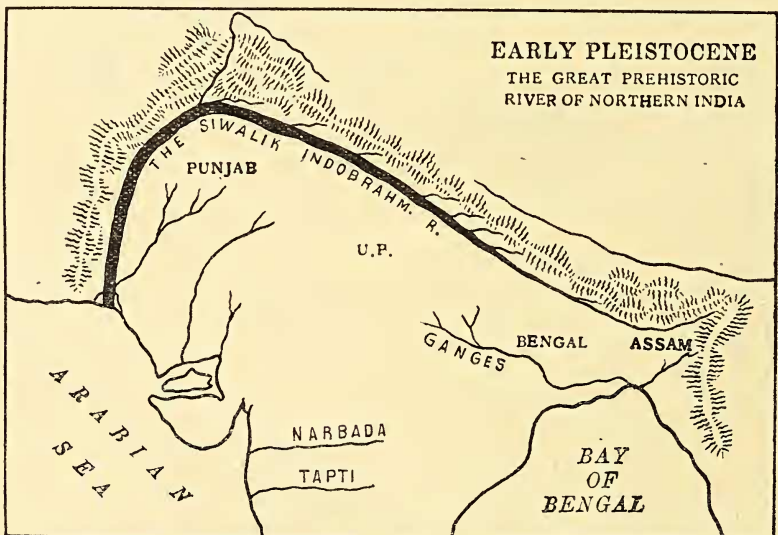


Fig. 10. The Indo-Brahm River during the early Pleistocene. After D. N. Wadia (*Proc. Nat. Inst. Sci. India*, 4, p. 389, 1938).

Siwalik Hills with its rich fossil fauna and flora. There is no fish distribution evidence at this period that there was an Indo-Brahm or Siwalik River as the fauna shows only extensive marshy conditions. As the sea receded westwards, this gulf must have become a continuous or a series of freshwater lakes, but during each Glacial period

of the Pleistocene, when precipitation was higher, evaporation was low and the run-off was greater, I presume this series of lakes may have joined again and run as a broad river draining towards the west and having its headwaters in Assam. Thus every Glacial period gave us a mighty, roaring Indo-Brahm River of the geologist. The ecological conditions during the Glacial periods brought into India the migrants from the east and the Indo-Brahm River helped to carry them to the extreme west of India.

On the northern side of the Himalayas also there was a similar longitudinal trough which dispersed the fish-fauna from south-west China to Seistan. There was also another longitudinal river at the base of the Vindhya-Satpura trend of mountains which helped in the distribution of the aquatic fauna to Peninsular India.

So far no racial studies have been carried out on the species common to the Indus and the Ganga river systems, but taxonomically they appear to be identical. Either there has been no significant change in the ecological conditions of the species since separation or the date of separation is so recent that marked racial differences have not yet had time to manifest themselves. It is believed by the geolo-

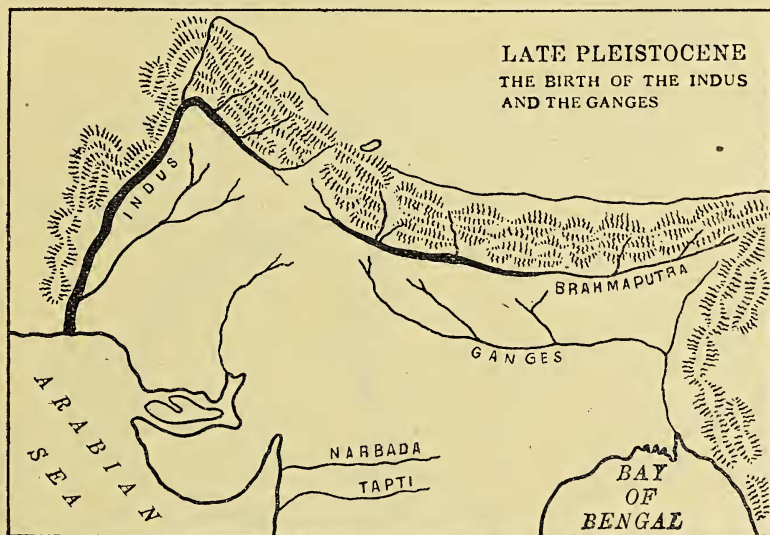


Fig. 11. The dismemberment of the Indo-Brahm River during the late Pleistocene. After D. N. Wadia (*Ibid.*, 4, p. 389, 1938).

gists that the dismemberment of the Indo-Brahm occurred in the late Pleistocene. There is some evidence for this belief from the fish distribution as is shown below.

ii. *Extension of the Indo-Gangetic fish-fauna into the Mahanadi and Godavari river systems.*—How did the fish-fauna of the Ganga migrate to the Mahanadi and colonise it? The greater part of the fish-fauna

common to the two rivers is that of the plains and not of the headwaters. The explanation of this riddle is to be found in the eustatic movements of the sea during the height of any Glacial period. The sea level fell by about 100 to 200 metres and vast stretches of the coastal shallow areas of the present-day seas became dry lands. The

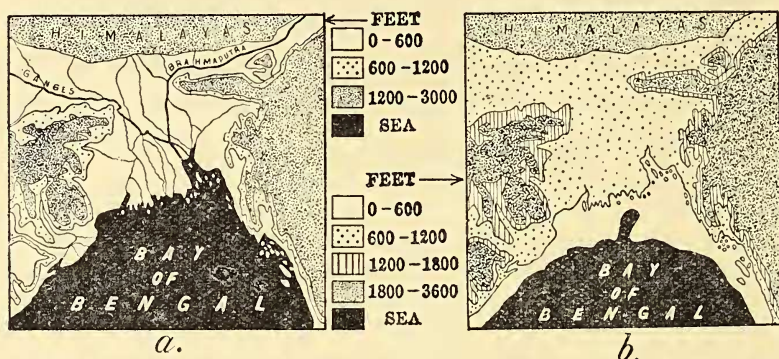


Fig. 12. The physiography of the Garo-Rajmahal Gap. (a) Present-day condition, (b) During the height of a Glacial Period. After S. L. Hora (*ibid.*, 17, p. 439, 1951).

Ganga, as is well-known historically, was flowing more towards the west. It seems that during the height of the Glacial periods, the Ganga and the Mahanadi may have formed a common delta thus

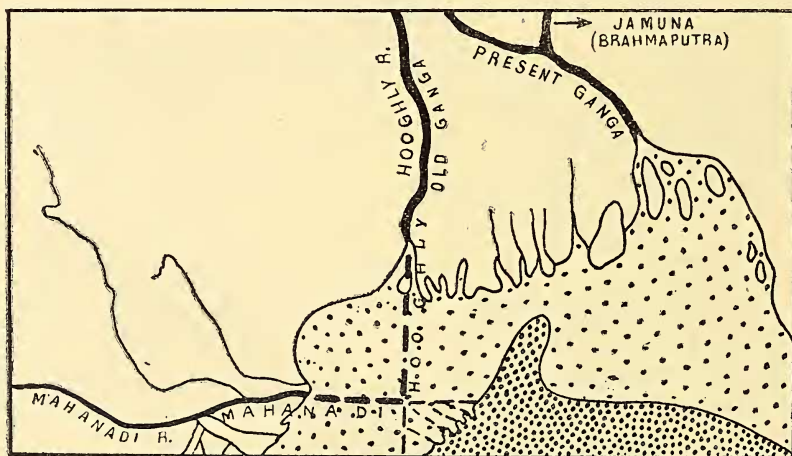


Fig. 13. The Lower courses of the Ganga and the Mahanadi during the height of a Glacial Period (Hypothetical).

permitting the fauna of the Ganga to colonise the bed of the Mahanadi.

During which Glacial period did this transference of fauna occur? The answer to this question in terms of Pleistocene geological events must be (a) after the dismemberment of the Indo-Brahm River and (b) after the tilting of the Peninsular block, for these two events resulted in the birth of the present-day Ganga and Mahanadi. So we are led to solve other problems before we can fix the date of the mixing of the waters of the Ganga and the Mahanadi.

I am indebted to Dr. M. S. Krishnan for the following chronology of the Pleistocene Glaciation:—

<i>Beginning of</i>	<i>End of last glaciation</i>	<i>Years ago</i>
<i>Last or 5th glaciation</i>		Ca. 10,000
	IV Interglacial period	„ 20,000
<i>4th glaciation</i>		„ 60,000
	III Interglacial period	„ 120,000
<i>3rd glaciation</i>		„ 180,000
	II Interglacial period	„ 250,000
<i>2nd glaciation</i>		„ 440,000
	I Interglacial period	„ 500,000
<i>1st glaciation</i>		„ 560,000
<i>Pleistocene</i>		„ 600,000
		„ 1,000,000

What factors caused these climatic variations is difficult to say and is outside the scope of this article. In a recent paper in the *Society's Journal* (Vol. 50, No. 4, p. 718, 1952) on 'The Climate of India', Banerji has stated:

'Post-glacial time falls into three main stages: first, a period of steadily increasing warmth, covering the establishment and decline of northern coniferous flora; next a long period of maximum warmth, marked by the dominance of deciduous forests; and finally an indication of decreasing warmth accompanied by gain of conifers at the expense of deciduous species. These results came from pollen analysis. There are minor variations, namely, return to warm conditions a thousand years ago and a present-trend to warmer and drier conditions, which may be no more than a passing phase. In producing these long-period changes some common cause was at work, which has also been changing more or less rhythmically. There has been much discussion over this common cause, but at present attention is centred mainly on the variations of the seasonal distribution of isolation in different latitudes through changes in the constants of the earth's orbit, the inclination of the earth's axis and the long-period changes in the solar radiation.'

I have quoted the above long passage to indicate that:

- i. Climatic changes and the resultant factors bring about vast changes in the ecology of organisms and induce speciation.

- ii. Biological objects can be good indicators of climatic variations in the past.
- iii. There is no stability so far as climate is concerned, there being short-period as well as long-period variations.

We have seen that there is no difference between the fish-faunas of the Indus and the Ganga River Systems and from this it can reasonably be inferred that their separation is of a recent date. Further, the fluviatile forms living in a more or less uniform environment are not likely to show a very rapid rate of speciation. Taking these two facts together, it would seem probable that the separation probably occurred during the third or fourth glaciation, at the most 250,000 years ago. The geologists also consider that the present drainage system of northern India was established during the Upper Pleistocene.

Due to the tilting of the Peninsular block, the species of the Western Ghats, as will be shown below, have got dispersed over a very wide area but so far as our studies have shown they have not yet become differentiated into subspecies or races. I have an intuitive feeling that the tilting of the Peninsula and the dismemberment of the Indo-Brahm were probably results of the same force and occurred simultaneously.

iii. *Occurrence of the so-called Malayan forms in the Western Ghats and the Satpura trend of mountains.*—The occurrence of the Malayan forms in the Western Ghats and other hill tops of peninsular India has been known for a long time. The most accepted explanation has been that both the Himalayan plants and animals retreated to the south during glaciation and during the interglacial periods went up to the hill tops to escape from the heat and dryness of the plains. This also accounts for their discontinuous distribution at the present time. Such a simple explanation could possibly fit in with the mode of dispersal of terrestrial animals and plants but could not account for the distribution of torrential fishes. Accordingly, the Satpura Hypothesis was proposed in 1937 and field studies proved some justification for the hypothesis. The main difficulty lay in the presence of the Garo-Rajmahal Gap which had to be crossed over to get access to the Satpura trend of mountains. The geological evidence concerning the age of the Gap was often discussed but proved to be ambiguous. However, it has now been found (Hora, 1951) that during each glacial period the level of the gap became several hundred feet higher relative to the sea level on account of eustatic movements of the sea (Text fig. 12). Owing to the increased precipitation, less evaporation and greater run-offs during the Glacial periods favourable ecological conditions were thus established for the dispersal of torrential fishes across the gap.

Extensive field investigations have shown (Menon, 1951) that the route of migration of the torrential fishes lay along the Satpuras and not along the Orissa Hills and the Eastern Ghats. From a detailed taxonomic study of the fish isolates in Peninsular India, Silas (1952) has found that there were 5 invasions corresponding to the

5 Glacial periods of the Pleistocene. I believe that the researches so far carried out in the Zoological Survey of India have supported the Satpura Hypothesis. The contribution of this hypothesis in regard to the dispersal of the terrestrial forms lies in the fact that the mountain ranges or hill tops developed favourable ecological conditions earlier and such conditions persisted there longer than in the plains. At all suitable heights favourable conditions persist up to the

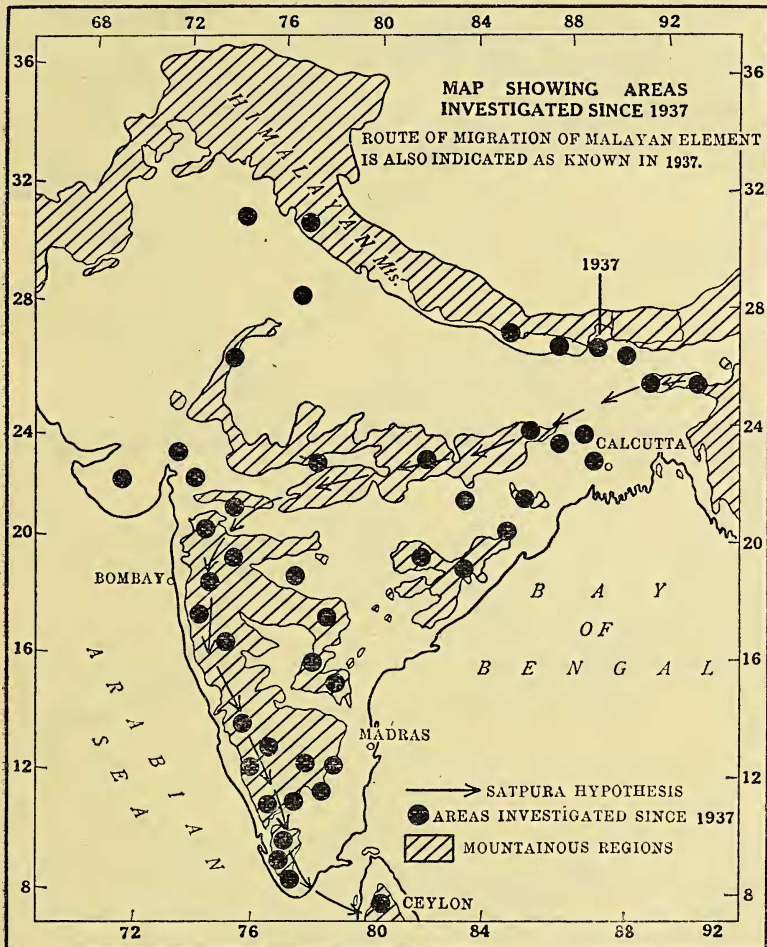


Fig. 14. Map of India to show the route of migration of the Malayan fishes and places of investigation in connection with the Satpura Hypothesis.

present and that is why the relict forms are now isolated on hill tops in Peninsular India.

iv. *Dispersal of the fish-fauna of the Western Ghats to the Eastern Ghats, Orissa Hills, Aravalli Range, Satpura and Vindhya Ranges.*—I

have referred above to the tilting of the Peninsular block during the late Pleistocene. Menon (1951) has dealt with this point exhaus-

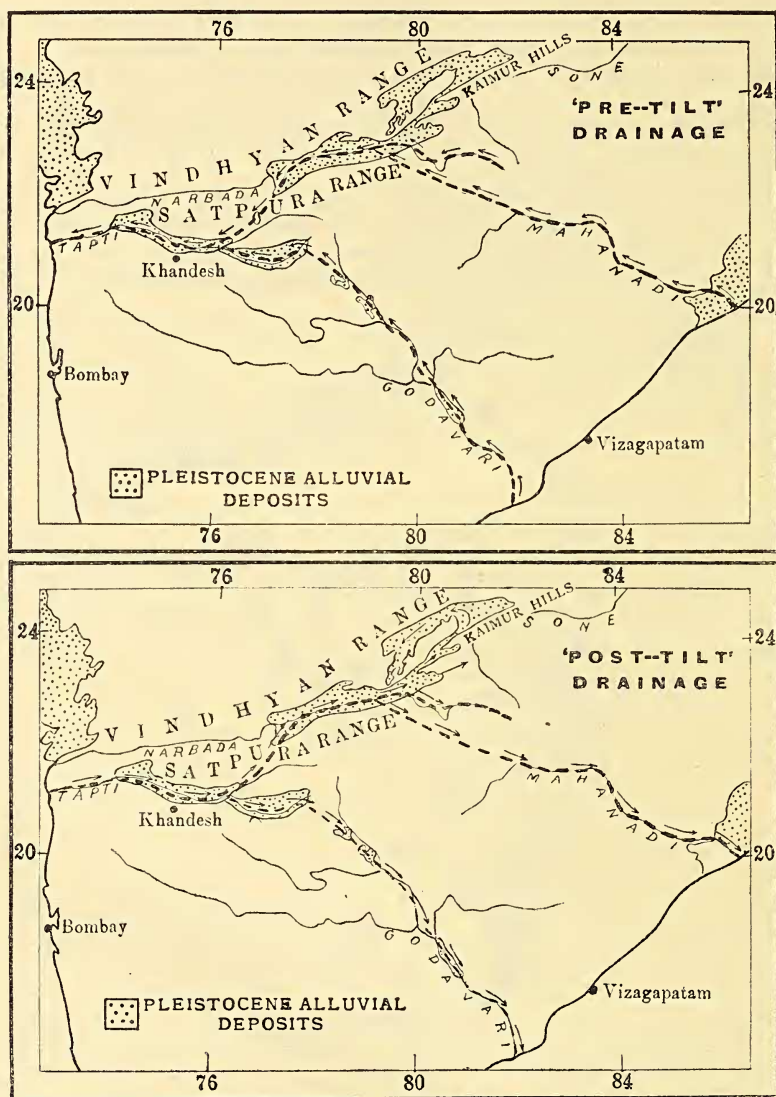


Fig. 15. Pre-tilt and Post-tilt drainage of Peninsular India. After A. G. K. Menon (*Proc. Nat. Inst. Sci. India*, 17, pp. 493-494, 1951).

tively and very lucidly so I propose to reproduce 3 of his drawings here which are self-explanatory. It is surmised that the tilting of the Peninsula occurred not more than 250,000 years ago and that

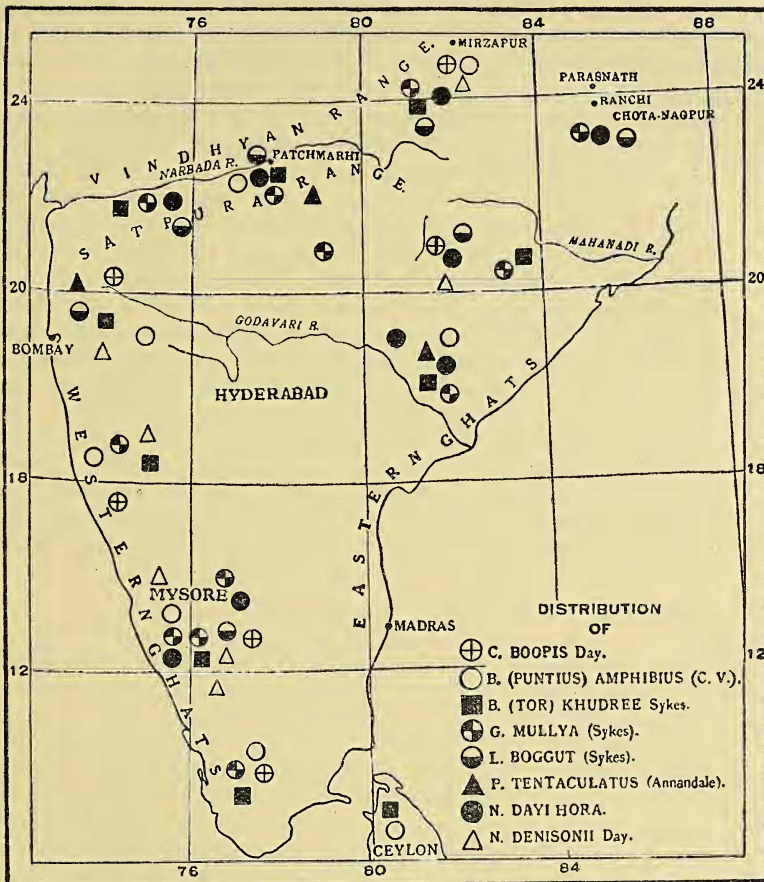


Fig. 16. Dispersal of the Western Ghats fishes as a result of the tilting of the Peninsula. After A. G. K. Menon (*ibid.*, 17, p. 495).

was probably contemporaneous with the dismemberment of the Indo-Brahm river.

v. *Occurrence of the Sind fish-fauna in the Aravalli Range.*—Hora and Mathur (1952) have dealt with this problem very recently. They have shown that a sunken ridge exists under the desert sand which may have been a regular chain of hills connecting the Sind Hills with the Aravalli Hills. It was probably along this chain that *Labeo nigripinnis* of the Sind Hills migrated to the Aravallis. This migration must have been, geologically speaking, quite recent as there appears to be no racial differentiation between the Sind and the Aravalli specimens. Such a migration may have been facilitated by the ecological conditions associated with the Glacial periods.

vi. *Absence of the so-called Malayan forms in the Western Himalayas.*—This problem is forcibly brought home to any one who studies the fauna and flora of the Himalayas. The so-called Malayan element

predominates as far as the Teesta drainage but thereafter towards the west it becomes less and less. It was this fact that made me propose the Satpura Hypothesis in 1937 in the following terms:

'As the Himalayas rose to a great height in the region of the isthmus (mostly the western part of the Assam Himalayas and eastern part of the Nepal Himalayas) all the evidence concerning the north-eastward extension of the Indo-Brahm seems to have been obliterated. The uplift movement was probably most active in this region as we find practically all the highest peaks of the Himalayas clustered round this area. This differential movement which probably occurred late in the Miocene period, must have obliterated all traces of the eastward extension of the Indo-Brahm and also acted as a barrier between the eastern and the western Himalayan fishes. *The new stocks of specialized hill-stream fishes from the east, not finding means to cross this barrier, were deflected towards south-west along the Satpura Trend which probably at that period stretched across India as a pronounced range from Gujarat to Assam Himalayas. From Gujarat the hill-stream fauna migrated towards the south along the Western Ghats and spread to the hills of the Peninsula in the extreme south.*

The portion of the above passage italicised now gives an idea of the original conception of the Satpura Hypothesis. Just as many of the original ideas had to be changed with regard to the Satpura Hypothesis in the light of further investigations, in the same way the above views with regard to the size of the Himalayas have undergone many changes. For instance, text fig. 7 shows that there was a transgression of the Bay of Bengal in the region of Assam from the late Eocene to the Pliocene. It would thus appear that the Assam and the Darjeeling Himalayas are features of the post-Pliocene physiography of India. In fact, it has now become clear that the Central Asian uplift is, geologically speaking, very recent (Hora, 1952). There is abundant geological evidence that there was another major uplift of the Himalayas after the Pliocene. It is during the Pleistocene period, therefore, that the marine, estuarine or freshwater marshy gap between India and the countries to the east and north seems to have been filled up. The monsoons as they are established in India today, could not have been established till their passage to the Central Asiatic region had been blocked by a mountainous barrier in the north-east. I am informed by Dr. S. K. Banerji that the south-west monsoon, in its present form, apparently commenced to be established at the close of the Würm glaciation. The present system of monsoon, according to Dr. Banerji, must have developed when the Himalayas attained a height of 10,000-15,000 ft., which is also roughly the depth of the south-west monsoon.

When the Pliocene Assam Gap in the Himalayas was filled up and the Himalayas had attained a height of 10,000-15,000 ft., only then could the monsoon rains produce torrential conditions in the Himalayas favouring the dispersal of the torrential fishes coming from the east. Evidently, this period is limited to about 20,000 years and thus there has not been sufficient time for the so-called Malayan

forms to spread their range westwards along the Himalayas. Our present studies have shown that a gradual spread westwards is taking place, for instance, *Amblyceps* has already gone as far as the Kangra Valley and *Psilorhynchus* as far as Delhi. Several other forms have been found in the Kosi and Gandak drainage systems. Mr. A. G. K. Menon is working on this problem and his results will be published shortly elsewhere.

CONCLUSION

I have so far discussed the fish geography of India, but now in conclusion I wish to point out in what respects advances have been made in elucidation of the palaeogeography of India.

The Assam Link.—During the Triassic period when there were only two large continents, the Angara and the Gondwana, separated from each other by seas for the greater part of their coast lines, there was a land connection between them over the Assam region. This connection seems to have persisted up to the upper Eocene when a transgression of the Bay of Bengal separated them. The marine gap thus created continued in existence till the Pliocene when brackishwater marshy conditions set in. The true land connection seems to have been established again in the Pleistocene but it was not until about 20,000 years ago that the Himalayas in this region covered the gap with high mountain ranges.

The Dismemberment of the Gondwana Continent.—The Gondwana Continent seems to have started breaking up in Eocene and by Upper Eocene Australia had separated off. Not very long after but still within the Upper Eocene, South America became separated from Africa. Though Africa also got separated from India for the greater part of its extent but retained a connection with India in the north-east, up to the middle pleistocene.

The Palaeo-Climates of India.—Both during the Upper Triassic and Jurassic periods there was intense desiccation so that all aquatic forms seem to have died out. Recolonization seems to have occurred again and again so long as the 'Assam Link' existed. The monsoon, as it is established at present, commenced only about 20,000 years ago when the Himalayas had attained a height of 10,000-15,000 ft. and the gap in the Assam region had been walled up. There were five well-defined periods of glaciation which gave India pluvial conditions and converted its plains into plateaux owing to the eustatic movements of the sea.

The Deccan Traps.—The lava flows, that have given us the Deccan Traps, seem to have commenced in the late Cretaceous period and continued at long intervals up to the Upper Eocene. They annihilated the flora and fauna during each active phase and the intervals between successive flows were of sufficiently long duration to permit of colonization by plants and animals.

The Peninsular Tilt and the Indo-Brahm.—It is postulated that the tilting of the Peninsular Block and the dismemberment of the Indo-Brahm occurred simultaneously about 250,000 years ago. The Mahanadi and the Godavari were flowing north-westwards before the tilt and the drainage of Assam then discharged into the large

river, the Indo-Brahm, that flowed into the Arabian sea. The Indo-Brahm River is shown to be a successor of the Siwalik Gulf, thus the two views of the geologists are reconciled. It is also postulated that the Ganga and the Mahanadi had a common delta during the last two phases of glaciation.

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